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EFFECTS OF FOREST PATCH SIZE ON NESTING SUCCESS OF WOOD THRUSHES

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Abstract.—Declines of many forest-dwelling Neotropical migrants have been attributed, in part, to fragmentation of forest habitat on the breeding grounds in North America. During 1990-1991, we determined reproductive success of Wood Thrushes (*Hylocichla mustelina*) nesting within contiguous forest habitat (>10,000 ha) and in nine forest fragments ranging in size from 9.2 to 126.5 ha in Berks County, Pennsylvania. We located 171 Wood Thrush nests. Nesting success differed significantly among forest size categories, with 86% of the nests successful in contiguous forest, 72% successful in large fragments (>100 ha), and 43% successful in small fragments (<80 ha). The variable that best predicted nest survival was forest area ($R^2 = 0.86$). Rates of predation differed significantly among forest size categories, and predation was the primary cause of nesting failure. We found 56% of the nests in small fragments were lost to predators as compared to 22% in large fragments and 10% within the contiguous forest. Visitation by mammalian predators to scent posts was significantly different between small and large forest sites (41 vs. 14%, respectively), and relative abundance of avian nest predators was significantly higher in small forest fragments than in the large forest sites ($\bar{x} = 1.04$ vs. 0.41 birds per census point). Brown-headed Cowbirds (*Molothrus ater*) parasitized 9% of the nests. Rates of brood parasitism did not differ significantly among forest size categories and had little influence on nesting success. Our results suggest that reproductive success of Wood Thrushes nesting within contiguous forest is high and that severe reproductive dysfunction as a result of high rates of nest predation is an important consequence of forest fragmentation. Received 6 July 1993, accepted 21 November 1993.

MANY FOREST-DWELLING NEOTROPICAL migrant songbirds have undergone population declines in eastern deciduous forests of North America (Robbins et al. 1989a, Askins et al. 1990). Most declining forest species are found less commonly than expected in small areas of forest than in large (area sensitive), and some of these songbirds have decreased in abundance or disappeared completely from small forest patches (Ambuel and Temple 1983, Blake and Karr 1984, Askins et al. 1987). Because forest fragmentation results in smaller forest patches or fragments separated from each other by nonforest habitat, these declines have been attributed, in part, to fragmentation of forest habitat in North America (Robbins 1979, Askins et al. 1990).

Numerous hypotheses have been proposed to explain why forest-dwelling Neotropical migrants decrease in abundance or disappear from small forest patches (Askins et al. 1990). As a forest becomes fragmented, the amount of edge habitat increases and the amount of interior de-

creases. Mammalian nest predators such as eastern chipmunks (*Tamias striatus*) and raccoons (*Procyon lotor*; Bider 1968, Forsyth and Smith 1973) tend to be more abundant along the forest edge than in the forest interior. Whitcomb et al. (1981) suggested that avian nest predators, such as Blue Jays (*Cyanocitta cristata*) and American Crows (*Corvus brachyrhynchos*), show a similar pattern. The Brown-headed Cowbird (*Molothrus ater*), a brood parasite, also is more abundant along edges (Brittingham and Temple 1983). In addition, rates of both nest depredation and brood parasitism are higher near forest edges than within the forest interior (Gates and Gysel 1978, Chasko and Gates 1982, Brittingham and Temple 1983, Temple and Cary 1988). Consequently, one hypothesis is that forest birds decline in number in small forest patches as a result of poor reproductive success due to high rates of predation on eggs and nestlings, and to brood parasitism (Brittingham and Temple 1983, Wilcove 1985, Askins et al. 1990).

Experiments with artificial nests indicate that nest predation is more frequent in small forest patches than within extensive areas of forest, thus supporting this hypothesis (Wilcove 1985,

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TABLE 1. Characteristics of 11 forest study sites and Wood Thrush nest success in Berks County, Pennsylvania, 1990-1991.

Study site	Forest area (ha)	Forest core area (ha) ^a	Distance to contiguous forest (km) ^b	Percentage forest area within 2-km radius ^c	Nest success ^d (n) ^e
Owl's Head	> 10,000 ^f	> 10,000	0.0	96.5	1.00 (258)
River of Rocks	> 10,000 ^f	> 10,000	0.0	97.2	0.72 (162)
Spitzenberg	126.5	45.3	2.4	35.7	0.72 (656)
Gun Club	103.4	47.8	10.6	50.5	0.65 (258)
Snook	79.8	6.5	11.2	42.7	0.33 (206)
Laudadio	40.4	10.0	8.2	29.0	0.43 (32)
Kunkle	23.4	2.5	9.1	20.9	0.29 (260)
Kehl	19.4	0.04	3.3	27.4	0.24 (94)
Lilienthal	18.7	1.4	11.8	42.7	0.35 (229)
Dixon	16.4	2.3	7.0	22.9	0.34 (287)
Bauscher	9.2	0.5	6.7	23.4	0.12 (96)

^a Area of forest > 100 m from an edge (Temple 1986).

^b Nearest forest > 10,000 ha.

^c Measured from center of each study site.

^d Nest-survival probability calculated by the Mayfield (1975) method for 1990 and 1991 combined.

^e Number of exposure days during both incubation and nestling period.

^f Nest searching occurred primarily within a 50-ha plot.

Small and Hunter 1988, Yahner and Scott 1988). However, artificial nests may not give an accurate estimate of rates of nest depredation (e.g. Martin 1987, Willebrand and Marcstrom 1988). In addition, since cowbirds locate nests to parasitize primarily by watching host nest-building activity (Thompson and Gottfried 1976), artificial nests cannot be used to measure rates of brood parasitism.

We determined reproductive success of Wood Thrushes (*Hylocichla mustelina*) nesting within contiguous forest and in forest fragments. We tested whether Wood Thrush nesting success, rates of nest depredation, and rates of brood parasitism varied with a variety of measurements of forest area or distance from the nearest forest edge. In addition, we tested whether the abundance of potential avian and mammalian nest predators and Brown-headed Cowbirds differed with forest patch size. We chose the Wood Thrush as a "model" species because it is an area-sensitive, forest-dwelling Neotropical migrant (Whitcomb et al. 1981, Robbins et al. 1989a) that has exhibited declines in number in the eastern United States (Holmes and Sherry 1988, Robbins et al. 1989b).

METHODS

Study sites.—We conducted our study from 1990-1991 in Berks County, Pennsylvania, on two areas within contiguous forest (> 10,000 ha) at Hawk Moun-

tain Sanctuary and nine forest fragments ranging in size from 9.2 to 126.5 ha (Table 1). The two areas within the contiguous forest were approximately 50 ha each and separated by approximately 1.5 km. All nine fragments were within 12 km of contiguous forest. We classified seven of the fragments as small (forest area < 80 ha) and two of the fragments as large (forest area > 100 ha). Our classification was somewhat arbitrary, but was based on both forest area and core area (area of forest at least 100 m from an edge; Temple 1986). For example, we decided to include Snook in the group of small fragments because of the low amount of core area (Table 1). Due to small samples sizes, for some of our analyses we combined data from the large fragments and contiguous forest and refer to them as large study sites.

The primary overstory of the study sites was mixed oak (*Quercus* spp.), with tulip poplar (*Liriodendron tulipifera*), American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), and black tupelo (*Nyssa sylvatica*) as characteristic species. Fragments were isolated from other forest habitat primarily by areas used for agriculture. A few suburban developments and highways also separated the fragments from other areas of forest. The area, core area, distance to contiguous forest, and percentage of forest area within a 2-km radius of the geometric center of each study site were measured from topographic maps and aerial photographs, respectively (Table 1).

Locating nests and determining nesting outcome.—We searched each study site extensively from May-August 1990-1991 to locate Wood Thrush nests. For the two years combined, we calculated the mean number of nests located per hectare for each study site as an index to nest density. We used a *t*-test to determine

whether our index to nest density differed between small fragments and large study sites (large fragments and contiguous plots combined). As nests were found, we determined their contents by using a convex mirror attached to a pole (Parker 1972). We used the pole and mirror to keep our contact with the nests at a minimum and to enable us to observe nests above eye level. We monitored nests every four days until the nesting process terminated either with nesting success (≥ 1 Wood Thrush young fledged) or nesting failure. We determined the fledgling date by visiting each nest approximately one or two days before the nestlings were to fledge (11–12 days old) and visiting the nest again the day after the expected fledgling date. Nest contents were not checked on days when inclement weather posed a threat to exposed eggs or nestlings.

We determined the frequency of brood parasitism based on the presence of either cowbird eggs or young in Wood Thrush nests. Because it is possible that cowbird eggs or young may disappear before nests are found, our rates of parasitism are minimum values. We determined the cause of nesting failure for all nesting attempts that were unsuccessful based on criterion used by Best and Stauffer (1980). Causes of nesting failure included: predation by large mammals; predation by small mammals, birds, or snakes; brood parasitism; nest abandonment; and weather.

We classified predation at nests into two general groups (large mammal; and small mammal, bird, or snake). Small mammals included all mammals up to the size of gray squirrels (*Sciurus carolinensis*; Best and Stauffer 1980). We tested whether rates of predation differed between years, between the egg and nestling periods, or among forest size categories for all nests. We tested whether rates of brood parasitism differed between years or among forest size categories.

Nesting success.—Nesting success was assessed by two methods. We determined the percentage of nests that were successful in small fragments, large fragments, and contiguous forest, and we tested whether nesting success differed among forest size categories or between years. Nesting success or nest-survival probability (NS) also was calculated on each study site using the Mayfield (1975) method. We compared the 1990, 1991, and combined 1990–1991 nest-survival probabilities for each study site to \log_{10} forest area (AREA), \log_{10} forest core area (CORE), arcsin transformation of the percent forest within 2-km radius (PFAS), and distance to contiguous forest (DTCF) of each study site. Variables were transformed to meet the assumptions of linear-regression analysis (Neter et al. 1990). Owl's Head and River of Rocks study sites were combined for these analyses because both sites are located within the same extensive forest and because of the small sample of nests. For the regression equations, we selected 500 ha of forest encompassing the two study plots and calculated the amount of core area (400 ha) within those 500 ha. We used backward-

stepwise-elimination regression analyses (SAS 1985) to develop models that included the variable(s) that best predicted nest survival. All four variables were initially entered into a model and removed if the variable did not meet a probability ($P < 0.10$).

Distance effect.—For each nest, we determined the distance from the nest to the nearest forest edge or opening 0.4 ha or larger, and grouped nests into three categories based on their distance from the edge (≤ 50 m, 51–100 m, and > 100 m). Edges were primarily abrupt field-forest edges or forest-road edges. We tested whether nesting success differed among distance categories for all Wood Thrush nests combined and for nests on small and large study sites. The comparison for nests found on small study sites was between only two distance categories (≤ 50 m and > 50 m) because there were only two nests that were more than 100 m from the nearest forest edge.

Determining relative abundance of avian nest predators.—A fixed-radius point-census method (Hutto et al. 1986) was used during the 1991 field season to determine the relative abundance of potential avian predators and Brown-headed Cowbirds (A. D. Dey, unpubl. data). Nine randomly selected survey points were established on each study site by placing a 150 \times 150 m grid over a map of each study site, numbering each grid point, and using a random numbers table. Survey points were separated by a minimum of 150 m to minimize the possibility of counting the same individual at different points and were located at least 60 m from the nearest edge. Each site was surveyed three mornings in late May and June, and all birds detected were recorded within a 60-m radius in a 5-min period. The maximum number of individuals of each species observed at each point during the three surveys was used as the estimate of relative abundance (Robbins et al. 1989a). The only potential avian nest predators detected were Blue Jays and American Crows. For each study site, the mean of the nine points was used as the measure of relative abundance of Blue Jays and American Crows on that study site. We used a Mann-Whitney test to determine if there was a difference in relative abundance of Blue Jays and American Crows between small and large study sites.

Scent-post survey of mammalian nest predators.—We conducted a scent-post survey on each of the study sites to determine activity levels of potential mammalian nest predators (Roughton and Sweeney 1982). During late July and early August in 1991, we randomly selected nine points on each study site that were at least 200 m apart and established scent posts. We selected random points by placing a grid over a map of each study site, numbering each grid point, and using a random numbers table. These survey points were not the same as the avian survey points. We monitored three posts per survey, with a one-week interval between surveys. We scraped away the leaf litter and smoothed the soil in a 1-m-diameter

TABLE 2. Percentage* of Wood Thrush nests that were successful, lost to predators, or parasitized by cowbirds in small fragments (<80 ha), large fragments (>100 ha), and within contiguous forest in Berks County, Pennsylvania, 1990-1991.

Nest fate	Forest fragments		Contiguous forest (21)	X ²
	Small (96 ^b)	Large (54)		
Successfully produced young	43	72	86	20.2***
Lost to predators	56	22	10	25.8***
Parasitized by cowbirds	13	2	10	4.9 ^{ns}

***, $P < 0.001$; **, $P > 0.05$

* Percentages do not add up to 100 because some failed nests are not included (e.g. loss to weather) and all parasitized nests were successful (e.g. fledged at least one host young).

^b Total number of nests.

circle for each scent post. We then applied a 0.6-cm coating of flour to the exposed ground. We dipped the cotton end of a 15-cm cotton swab in fatty-acid scent (FAS; Roughton 1982) and pressed the wooden end of the swab into the ground in the center of the circle. After a 24-h period, we returned to the scent post and determined the animals that had visited the post by identifying tracks. We used the scent posts only when there was no precipitation during the 24-h period between scent-post establishment and our return visit. We tested whether the frequency of mammalian visitation to the scent posts differed between the small and large study sites.

RESULTS

Nesting success.—We found 44 Wood Thrush nests in 1990 and 127 in 1991, including 96 nests in small forest fragments (<80 ha), 54 in large fragments (>100 ha), and 21 within contiguous forest (Table 2). The number of nests located per hectare differed ($t = -1.93$, $df = 9$, $P = 0.09$) between small ($n = 7$, $\bar{X} = 0.37 \pm SE$ of 0.1) and large ($n = 4$, $\bar{X} = 0.11 \pm 0.02$; large fragments and contiguous forest plots combined) study sites. The earliest nest initiation (date when female began incubation) was during mid-May on both the small and large study sites in both years. There was no difference ($X^2 = 0.01$, $df = 1$, $P > 0.90$) in the percentage of successful nests between 1990 and 1991 on the small study sites (42 vs. 43%; $n = 31$ and 65, respectively) or on the large (large fragments and contiguous forest) study sites (69 vs. 77%; $n = 13$ and 62, respectively; $X^2 = 0.39$, $df = 1$, $P > 0.50$). The

TABLE 3. Pearson correlation coefficients of forest size variables and Wood Thrush nesting success on 10 study sites in Berks County, Pennsylvania, 1990-1991.

Variable	Nesting success	AREA	CORE	PFAS
AREA	0.93*			
CORE	0.89*	0.87*		
PFAS	0.79*	0.83*	0.72*	
DTCF	-0.47	-0.42	-0.21	-0.43

*, $P < 0.05$.

percentage of successful nests differed significantly among forest size categories and was highest within the contiguous forest (Table 2).

Nest-survival probabilities ranged from 0.12 to 0.43 in the small forest fragments, and were more than 0.65 in the large fragments and contiguous forest (Table 1). Nest-survival probabilities were positively correlated with forest area, forest core area, and percent forest within a 2-km radius of each study site, and all three measurements of forest area were highly correlated with each other (Table 3). The best models for predicting Wood Thrush nest survival in 1990, 1991, and 1990-1991 were all one-variable models, and included either forest area or core area (Table 4, Fig. 1).

Nesting failure and brood parasitism.—Nest abandonment caused one nesting failure in 1990, and weather caused one nesting failure in 1990 and one in 1991. Wood Thrush nesting failure was caused by predation 95% or more of the time in both years. We attributed 78% of the losses to small-mammal, bird, or snake nest predators, and 22% to large mammals. On four separate occasions, we observed Common Grackles (*Quiscalus quiscula*) preying on all of the eggs in four different Wood Thrush nests. We were unable to identify positively the species of nest predators in other instances. We observed Wood Thrushes aggressively chasing Blue Jays on several occasions and found Blue Jay nests on all of the small study sites in both years, but on none of the large study sites.

Predation at nests was not significantly different ($X^2 = 0.60$, $df = 1$, $P > 0.25$) between years for nests in the small study sites (55 vs. 63%, respectively), or for Wood Thrush nests located in the large (large fragments and contiguous forest) study sites (15 vs. 19%; $X^2 = 0.11$, $df = 1$, $P > 0.50$). Nest predation differed significantly among forest size categories and was lowest within the contiguous forest (Table 2).

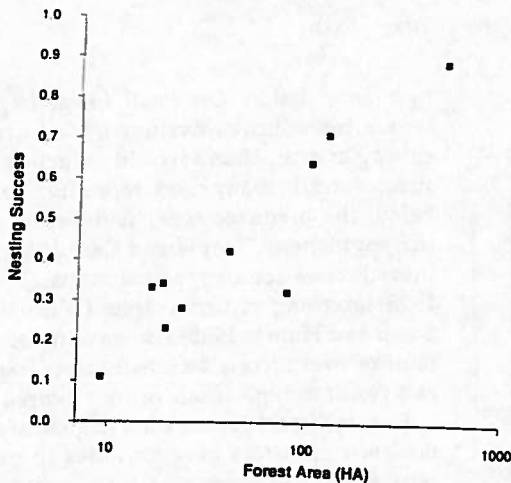


Fig 1. Relationship between Wood Thrush nesting success (1990-1991 combined) and forest patch size on 10 study sites, Berks County, Pennsylvania ($R^2 = 0.86$, $P < 0.001$).

Predation at nests was significantly different ($X^2 = 4.26$, $df = 1$, $P < 0.05$) between the incubation ($n = 139$) and nestling ($n = 126$) periods (31 vs. 20%) for all Wood Thrush nests combined, but was not significantly different ($X^2 = 1.55$, $df = 1$, $P > 0.1$) between periods for nests on the small study sites (42 vs. 32%; $n = 80$ and 62, respectively) or for nests on the large study sites (15 vs. 8%; $n = 59$ and 64, respectively; $X^2 = 1.69$, $df = 1$, $P > 0.1$).

Brood parasitism of Wood Thrush nests was significantly different ($X^2 = 6.55$, $df = 1$, $P < 0.025$) between 1990 and 1991 (18 vs 6%) for all Wood Thrush nests combined. Brood parasitism was not significantly different ($X^2 = 0.55$, $df = 1$, $P > 0.25$) between 1990 and 1991 (16 vs. 11%) on the small study sites but was significantly different ($X^2 = 14.90$, $df = 1$, $P < 0.001$) between years (23 vs. 0%) on the large study sites. Brood parasitism did not differ significantly among the forest size classes (Table 2), and brood parasitism never caused total nest failure.

TABLE 4. Best models for predicting Wood Thrush nesting success in 1990, 1991, and 1990-1991 on 10 study sites in Berks County, Pennsylvania.

Year	Model	R^2	F
1990	NS = $0.29 + 0.22$ (CORE)	0.68	16.75**
1991	NS = $-0.26 + 0.43$ (AREA)	0.90	66.24***
1990-1991	NS = $-0.26 + 0.43$ (AREA)	0.86	48.52***

** $P < 0.01$. *** $P < 0.001$.

TABLE 5. Species visiting predator scent posts located on study sites in Berks County, Pennsylvania, 1991.

Predator	No. posts visited	Percent of total visits
Raccoon (<i>Procyon lotor</i>)*	11	34.4
Virginia opossum (<i>Didelphis virginiana</i>)*	7	21.9
House cat (<i>Felis silvestris</i>)*	5	15.6
Striped skunk (<i>Mephitis mephitis</i>)	3	9.4
Eastern chipmunk (<i>Tamias striatus</i>)*	3	9.4
Weasel spp. (<i>Mustela</i> spp.)*	2	6.2
Dog (<i>Canis familiaris</i>)	1	3.1
Total	32	100.0

* Nest predators that climb trees.

Relative abundance of avian nest predators and cowbirds.—Relative abundance of Blue Jays and American Crows ranged from 0.44 to 1.44 birds per census point on the small study sites ($n = 5$) and from 0.33 to 0.44 on the large sites ($n = 4$). Mean relative abundance of Blue Jays and American Crows was significantly higher (Mann-Whitney $W = 11.5$, $P = 0.04$, adjusted for ties) on the small study sites ($\bar{x} = 1.04 \pm 0.17$) than on the large ($\bar{x} = 0.41 \pm 0.03$). Although we occasionally observed Common Grackles and Brown-headed Cowbirds on our sites, none were detected during the censuses.

Abundance of mammalian nest predators.—Visitation by all potential mammalian nest predators to scent posts was significantly different ($X^2 = 7.42$, $df = 1$, $P < 0.01$) between scent posts in small ($n = 54$) and large ($n = 36$) study sites (41 vs. 14%). Of the species that visited the scent posts, the raccoon was most common and accounted for 34% of all visits (Table 5). Visitation by tree-climbing mammalian nest predators (those that are able to prey on Wood Thrush nest contents) to scent posts was also significantly different ($X^2 = 13.67$, $df = 1$, $P < 0.001$) between small and large study sites (41 vs. 6%).

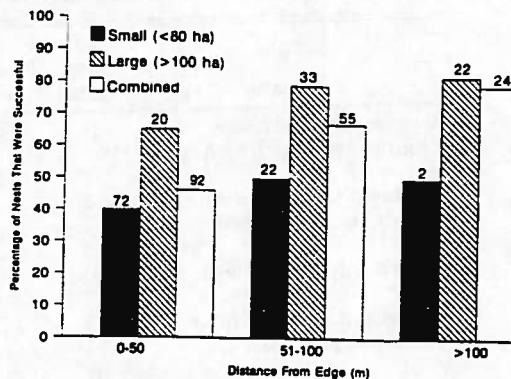


Fig. 2. Percentage of Wood Thrush nests (1990-1991 combined) that were successful and distance from an edge on small (<80 ha), large (>100 ha), and combined (both small and large) forest study sites. Numbers of nests per group are given at top of each bar.

Edge effect.—With all nests combined, nesting success differed significantly ($X^2 = 11.10$, $df = 2$, $P < 0.01$) with distance from edge and was 46% within 50 m of the edge, 67% for nests located 50 to 100 m from the edge, and 79% for nests located more than 100 m from the edge (Fig. 2). When analyzing within forest size categories, nesting success was not significantly different ($X^2 = 0.78$, $df = 1$, $P > 0.10$; Fig. 2) between nests located less than 50 m from the forest edge and those located farther away on the small study sites or among the three distance categories on the large study sites ($X^2 = 1.88$, $df = 2$, $P > 0.10$; Fig. 2).

DISCUSSION

Nesting success and predation.—Nesting success of Wood Thrushes within the large contiguous areas of forest and on the large forest fragments was well above the level needed to balance expected mortality rates (Temple and Cary 1988). Our results are in accord with those of Holmes et al. (1992), who measured the nesting success of Black-throated Blue Warblers (*Dendroica caerulescens*) nesting in unfragmented habitats in New Hampshire. Results of both studies suggest that nest success of Neotropical migrants nesting in unfragmented forest habitats is high and well above the level currently reported for birds nesting in fragmented habitats (e.g. Martin 1992, Robinson 1992, Porne-luzi et al. 1993).

As forest patch size declined, nest success also declined, primarily as a result of high rates of

nest depredation. On small forest fragments, severe reproductive dysfunction occurred, resulting in as much as a sixfold reduction in nest success and, in many cases, reproductive output below the predicted level required to sustain the population (Temple and Cary 1988). Other investigators locating actual nests (Robinson 1992) or using artificial nests (Wilcove 1985, Small and Hunter 1988) also have reported low rates of nest success on small forest fragments as a result of high levels of nest depredation.

The scent-post survey used to quantify mammal nest predators gave an index to predator activity, but did not enable us to measure abundance or to identify specific nest predators at specific nests. The point counts used to quantify avian predators should provide an index to abundance, but we were skeptical of their accuracy because the behavior of many nest predators may have made them difficult to detect with point counts. For example, Common Grackles often moved through the woods without calling, and we observed grackles preying on eggs, yet never detected them with the point counts. Despite these shortcomings, high rates of nest depredation on small fragments were associated with a greater abundance or activity level of potential nest predators. Similarly, Angelstam (1986) found that high rates of depredation on artificial nests were associated with a greater abundance of nest predators and that the rate of depredation by any particular predator varied in proportion to its relative abundance.

One explanation for higher rates of predation at nests in small woodlots is that small woodlots support few large predators that may regulate populations of smaller nest predators (Whitcomb et al. 1981). In addition, the habitat surrounding the fragments may support high populations of nest predators that also forage within the forest patch. Several species of mammal nest predators are more abundant along the forest edge than in the forest interior (Bider 1968, Forsyth and Smith 1973); Robbins (1980) and Whitcomb et al. (1981) suggested that avian predators show a similar pattern. The small tracts of forest in our study could be considered as mostly edge habitat, which may explain why both abundance of nest predators and rates of nest depredation were higher on the small tracts of forest than on the larger tracts.

The abundance of Wood Thrush was not correlated with forest area (Hoover 1992), but our

index to nest density was higher on small fragments than on the large sites. We suspect that this difference is due to a larger number of re-nests on small sites as birds whose nests were destroyed by predators nested a second time. We were aware of birds re-nesting, but we did not color-band females so we cannot estimate the percentage of nests that were second attempts.

Edge effects.—One way forest fragmentation is presumed to affect nesting success is through edge effects with elevated rates of predation, brood parasitism, or both near the interface of a forest and an adjacent opening (Gates and Gysel 1978, Ambuel and Temple 1983, Brittingham and Temple 1983, Askins et al. 1990). In our study, nest success increased with distance from edge for all nests combined. However, when we grouped nests into separate forest size categories (small and large), the trend was not significant. Other researchers also have failed to detect differential nest success with distance from edge (Angelstam 1986, Small and Hunter 1988, Yahner and Scott 1988, Robinson 1990).

Because our small fragments were almost exclusively edge habitat and most nests were close to the edge, we could not make a valid comparison between nest success and distance from the edge on those sites. On the large fragments and contiguous forest, rates of nest predation were low and nest success high throughout. Perhaps the occurrence of edge related changes in rates of nest predation depends on the local density of nest predators. This apparently is the case for rates of brood parasitism. In areas where cowbird populations are high, parasitism rates are high throughout forested areas regardless of distance from edge (Robinson 1990). In areas where cowbird numbers are low, levels of parasitism are low throughout (our study). It is primarily at intermediate densities that edge effects are apparent (Brittingham and Temple 1983).

Brood parasitism.—In contrast to results from the midwestern United States (Brittingham and Temple 1983, Robinson 1992), rates of brood parasitism by Brown-headed Cowbirds were low and in no case responsible for total nest failure. Roth and Johnson (1993) reported similar results from Delaware, and Holmes et al. (1992) reported no parasitism of Black-throated Blue Warblers nesting in unfragmented habitats in New Hampshire, nor did they observe cowbirds

on their sites. Apparently, there is much regional variation in the rates and intensity of brood parasitism, and in the influence it has on songbird reproduction (Hoover and Brittingham 1993).

Rates of cowbird parasitism varied temporally and were higher in 1990 than in 1991. Roth and Johnson (1993) also noted temporal variation in rates of parasitism during the 17 years of their study. We suspect that the higher rates of brood parasitism in 1990 than in 1991 were probably associated with gypsy moth (*Lymantria dispar*) defoliation. During the summer of 1990, defoliation by gypsy moths was almost complete on our contiguous forest sites. During 1991, defoliation was minimal on all sites. This factor potentially influences rates of cowbird parasitism in a number of ways. By removing leaf cover, it may make nests more visible and easier for cowbirds to locate. However, other researchers have not reported a relationship between nest concealment and probability of parasitism (Anderson and Storer 1976, Buech 1982). Alternatively, because cowbirds use tall exposed snags for displaying and nest searching (Mayfield 1965), areas defoliated by gypsy moths may attract cowbirds by providing an abundance of exposed perches. In addition, because cowbirds generally are less abundant within forests than open areas (Friedmann 1929, Mayfield 1965, Brittingham and Temple 1983), gypsy moth defoliation may make the habitat more suitable for cowbirds by opening the forest. Finally, cowbirds may become more abundant during gypsy moth outbreaks because they prey on the moth caterpillars and are attracted to high density gypsy moth areas (Smith and Lautenschlager 1981).

Minimum-area requirements.—Minimum-area requirements have been determined for Wood Thrushes and other Neotropical migrants by comparing either presence-absence or abundance of that particular species on fragments of different sizes (e.g. Robbins et al. 1989a). This method is useful in predicting where a species might occur, but it may give misleading results if one assumes that presence or even abundance reflects habitat quality. For a number of reasons, the abundance of a particular species may not be a true reflection of habitat quality (Van Horne 1983, Pulliam 1988). Apparently, this is the case with many Neotropical migrants which continue to breed in "sink" habitats where reproduction is well below the level needed to sustain

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the population (e.g. Robinson 1992). For example, Robbins et al. (1989a) found a 70% probability of detecting Wood Thrushes on fragments in the 10 to 30 ha range. However, we found nesting success on fragments of that size was less than 35%. Robbins et al. (1989a) concluded that the minimum-area requirement for breeding Wood Thrushes was 1 ha, but we have shown that nesting success on fragments of that size would be extremely low. In addition, Villard et al. (1992) showed that small fragments, although frequently occupied by Wood Thrush, were more likely to undergo local extinctions than large forested areas and suggested that small fragments may represent population "sinks." For Neotropical migrants, using data on reproductive success in conjunction with relative abundance is needed to determine true minimum-area requirements.

In addition to forest area, the amount of core area was correlated with nesting success. Temple (1986) found that forest core area was a better predictor than forest area of whether Wood Thrush and many other Neotropical migrants were present on a particular fragment. In our study, forest area and core area were highly correlated ($r = 0.87$) making it difficult to separate the relative importance of each. However, we had one relatively large but narrow (area = 79.8 ha, core area = 6.5 ha) site included in our study. Nesting success on this site was low and comparable to areas less than 20 ha, suggesting that amount of core area is important. Wilcove (1985) also observed high rates of nest predation on one of his large sites and suggested that high rates of predation occurred because of the long narrow shape of the forest. The relationship between forest core area and nesting success suggests that forest fragments should be managed to maximize forest core area.

Although small forest patches do not provide the quality of habitat of extensive areas of forest, they should not be dismissed as unimportant. Small forest patches, even when demographic "sinks," may contribute positively to the long-term persistence of the larger metapopulation (Howe et al. 1991). In addition, reproductive success in some small woodlots is high enough to sustain populations at least during some years (Roth and Johnson 1993).

Forest fragmentation and Neotropical migrants.— We have taken one demographic parameter, reproductive success, and shown how it varied across a landscape depending on forest patch

size. Our results suggest that in areas where forests are fragmented by agriculture or suburban development, reproductive success of Neotropical migrants will be low. Other researchers have hypothesized that reproductive success and productivity are the primary factors determining subsequent population size and population trends for these species (Holmes et al. 1992, Sherry and Holmes 1992, Roth and Johnson 1993). If this is the case, Pennsylvania and other eastern areas that still retain extensive areas of contiguous forest habitat hold the key for the future of many forest-dwelling Neotropical migrants, and efforts should be made to retain these areas as contiguous tracts of forest with minimal fragmentation by roads, agriculture, or suburban development.

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index to nest density was higher on small fragments than on the large sites. We suspect that this difference is due to a larger number of re-nests on small sites as birds whose nests were destroyed by predators nested a second time. We were aware of birds re-nesting, but we did not color-band females so we cannot estimate the percentage of nests that were second attempts.

Edge effects.—One way forest fragmentation is presumed to affect nesting success is through edge effects with elevated rates of predation, brood parasitism, or both near the interface of a forest and an adjacent opening (Gates and Gysel 1978, Ambuel and Temple 1983, Brittingham and Temple 1983, Askins et al. 1990). In our study, nest success increased with distance from edge for all nests combined. However, when we grouped nests into separate forest size categories (small and large), the trend was not significant. Other researchers also have failed to detect differential nest success with distance from edge (Angelstam 1986, Small and Hunter 1988, Yahner and Scott 1988, Robinson 1990).

Because our small fragments were almost exclusively edge habitat and most nests were close to the edge, we could not make a valid comparison between nest success and distance from the edge on those sites. On the large fragments and contiguous forest, rates of nest predation were low and nest success high throughout. Perhaps the occurrence of edge related changes in rates of nest predation depends on the local density of nest predators. This apparently is the case for rates of brood parasitism. In areas where cowbird populations are high, parasitism rates are high throughout forested areas regardless of distance from edge (Robinson 1990). In areas where cowbird numbers are low, levels of parasitism are low throughout (our study). It is primarily at intermediate densities that edge effects are apparent (Brittingham and Temple 1983).

Brood parasitism.—In contrast to results from the midwestern United States (Brittingham and Temple 1983, Robinson 1992), rates of brood parasitism by Brown-headed Cowbirds were low and in no case responsible for total nest failure. Roth and Johnson (1993) reported similar results from Delaware, and Holmes et al. (1992) reported no parasitism of Black-throated Blue Warblers nesting in unfragmented habitats in New Hampshire, nor did they observe cowbirds

on their sites. Apparently, there is much regional variation in the rates and intensity of brood parasitism, and in the influence it has on songbird reproduction (Hoover and Brittingham 1993).

Rates of cowbird parasitism varied temporally and were higher in 1990 than in 1991. Roth and Johnson (1993) also noted temporal variation in rates of parasitism during the 17 years of their study. We suspect that the higher rates of brood parasitism in 1990 than in 1991 were probably associated with gypsy moth (*Lymantria dispar*) defoliation. During the summer of 1990, defoliation by gypsy moths was almost complete on our contiguous forest sites. During 1991, defoliation was minimal on all sites. This factor potentially influences rates of cowbird parasitism in a number of ways. By removing leaf cover, it may make nests more visible and easier for cowbirds to locate. However, other researchers have not reported a relationship between nest concealment and probability of parasitism (Anderson and Storer 1976, Buech 1982). Alternatively, because cowbirds use tall exposed snags for displaying and nest searching (Mayfield 1965), areas defoliated by gypsy moths may attract cowbirds by providing an abundance of exposed perches. In addition, because cowbirds generally are less abundant within forests than open areas (Friedmann 1929, Mayfield 1965, Brittingham and Temple 1983), gypsy moth defoliation may make the habitat more suitable for cowbirds by opening the forest. Finally, cowbirds may become more abundant during gypsy moth outbreaks because they prey on the moth caterpillars and are attracted to high density gypsy moth areas (Smith and Lautenschlager 1981).

Minimum-area requirements.—Minimum-area requirements have been determined for Wood Thrushes and other Neotropical migrants by comparing either presence-absence or abundance of that particular species on fragments of different sizes (e.g. Robbins et al. 1989a). This method is useful in predicting where a species might occur, but it may give misleading results if one assumes that presence or even abundance reflects habitat quality. For a number of reasons, the abundance of a particular species may not be a true reflection of habitat quality (Van Horne 1983, Pulliam 1988). Apparently, this is the case with many Neotropical migrants which continue to breed in "sink" habitats where reproduction is well below the level needed to sustain

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